THE DISPERSAL OF *CULICOIDES MOHAVE* (DIPTERA: CERATOPOGONIDAE) IN THE DESERT OF SOUTHERN CALIFORNIA

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ABSTRACT. The dispersal of *Culicoides mohave* was studied near the Salton Sea in the lower desert of southern California. Preliminary observations indicated that host-seeking females were most active immediately after sunset and immediately before sunrise. A mark-release-recapture technique was used to document a mean distance traveled of 1.2 km, in 12 hr (the first flight period) and a cumulative distance of 1.94 km after 30 hr (following the second and third flight periods). Nearly 14% of 20,646 marked females were recaptured. Although the mass of the population moved with the prevailing wind, many females dispersed against it, one as far as 6.0 km in 30 hr. Unmarked females were captured at all trapping locations in the Salton Sea basin (up to 4.59 km from the larval habitat), but their numbers diminished precipitously 2.5 km beyond the shoreline.

INTRODUCTION

The Salton Sea is a saline body of water 72 m below sea level in the arid Coachella Valley of southern California. Perennially warm temperatures and marshy shorelines provide a suitable larval habitat for many ceratopogonids (Wirth 1952, Clastrier and Wirth 1978, Wirth and Atchley 1973). While studying the biology of *Leptoconops* spp., we encountered large populations of a host-seeking ceratopogonid, *Culicoides mohave* Wirth. This is a minute (±1.2 mm long) hematophagous midge whose larval development is probably restricted to the shoreline of inland saline waters in California and Arizona (Wirth and Moraes 1979, Wirth, personal communication). Preliminary observations indicated that this species was abundant throughout the desert of the Salton Sea basin. Host-seeking females were universally anthrone positive (Van Handel 1972), indicating recent imbibition of nectar and suggesting the potential for dispersal. Consequently, we made a pilot study to examine the characteristics of dispersal in populations of *C. mohave*.

MATERIALS AND METHODS

Throughout this study the activity and dispersal of *C. mohave* females were quantified by using unlit miniature surveillance traps baited with dry ice as described by Brenner et al. (1984). Preliminary trials showed that this trap almost exclusively attracted unfed mated females with resting stage ovarioles. These females readily fed when offered an arm; hence, we refer to females collected in these traps as "host-seeking." In paired tests, traps placed at ground level collected significantly more midges than traps at 2 m (Brenner et al. 1984). Consequently, all traps were placed at ground level during our study.

Preliminary observations indicated that this species was not active during the day. To determine more precisely when host-seeking midges were most active, the circadian activity of *C. mohave* was monitored during August 24–25, 1981. Collection bags of continuously-operated traps were changed every 1 or 2 hours. Three traps were used, 1 each at 5 m, 110 m and 1.1 km from the Salton Sea; dry ice was replenished every 6 hr. Dry bulb and wet bulb temperatures and wind velocity were recorded at each change of collection bags.

The dispersal of *C. mohave* was studied using a mark-release-recapture method. Host-seeking females were trapped 750 m from the Salton Sea from 1600 to 2000 hr and were immediately transported to the site of release where they were anaesthetized briefly with CO_2 and passed through a coarse sieve to eliminate larger insects. Species composition was determined from random samples of a few hundred adults. Those remaining were counted volumetrically and placed in a 0.47 liter cardboard container whose internal surfaces had been coated with 0.2 gm of fluorescent powder.[4] After securing the lid, the carton was revolved slowly to mark the adults. Midges were released immediately; at 12 hr post-release the carton was recovered, the number of dead ceratopogonids was determined, and subtracted from the number marked.

A preliminary trial was conducted involving the release of 5,523 orange-marked females 50 m from the Salton Sea. Thirteen traps positioned in 3 transects, each extending 1.5 km from a common point, recaptured 21% within 12 hr; 9.3% of those were taken 1.5 km from

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the release point. Consequently, our study was devised to encompass a larger area.

In preparation for the placement of traps, we drew concentric rings on a topographic map with radii at 0.5 km intervals (Fig. 1). The center of these circles was located 3.25 km north of the Salton Sea in an area of unimproved desert. We selected 25 points on the rings as desirable locations for the placement of traps. Twenty were located on the first 3 rings (0.5—1.5 km) and were spaced fairly evenly on each ring. The remaining 5 points, on rings 4, 5 and 6 (2.0–3.0 km) were positioned on a NW-SSE axis which represented the direction of prevailing wind in the area. A continuously-recording weather station measured wind speed and direction and temperature at the center of the rings.

On September 29, 1981, traps were emplaced during 1700–2400 hr. Host-seeking females (to be marked) were collected in 6 additional traps placed 750 m from the Salton Sea. These were separated into 2 groups, marked, and released at 0100 hr (September 30) in the center of the rings (red), SSE of the concentric circles 50 m from the Salton Sea (orange). Thus, this latter group was released 1.2 km SSE of the furthest trap on the last ring (Fig. 2); these midges would allow measure of flight against prevailing wind.

Traps were operated continuously for 30 hr from the time of release. After 12 hr the collection bags were changed, batteries were replaced, and dry ice was replenished. All collection bags were transported to the laboratory on dry ice where midges were placed on a black background and examined under longwave ultraviolet light for fluorescence. The number marked and the total number captured (determined volumetrically) were recorded; marked specimens other than *C. mohave* [*C. variipennis* (Coq.) and *Leptoconops* spp.] were counted and discarded. The species composition was determined to quantify the number of unmarked *C. mohave* females captured.

The method of determining the mean distance traveled (MDT) per time interval was that of Lillie et al. (1981). Briefly, the rationale and procedures are as follows. The calculations for determining MDT are dependent on the density of traps. In our study, since 4 traps were used in ring 1 (0.5 km), then 43 traps would have been necessary to ensure equal trap density in ring 6 (1 trap per 0.2 km^2) and 141 traps would have been required for this study. The logistics of such a project would have been overwhelming; consequently, we used fewer traps on the outer rings. Therefore, correction factors were computed for each ring to eliminate the disparity in trap density, thereby enabling us to estimate the density of marked midges per equal trapping area. The formula for determining the correction factor (CF) for each ring is:

$$CF = A_r/A_t \times N_p$$

where A_r = area of trap ring, A_t = total trapping area, and N_p = number of traps used per sampling period. These CF values were used to determine the corrected mean number recaptured per trap ring.

The mean distance traveled per sampling period was computed using the following formula:

$$MDT = (\overline{X}_c \times r)/\Sigma\overline{X}_c$$

where $\overline{X}_c$ = corrected mean number recaptured per ring, and r = radius of the ring (km).

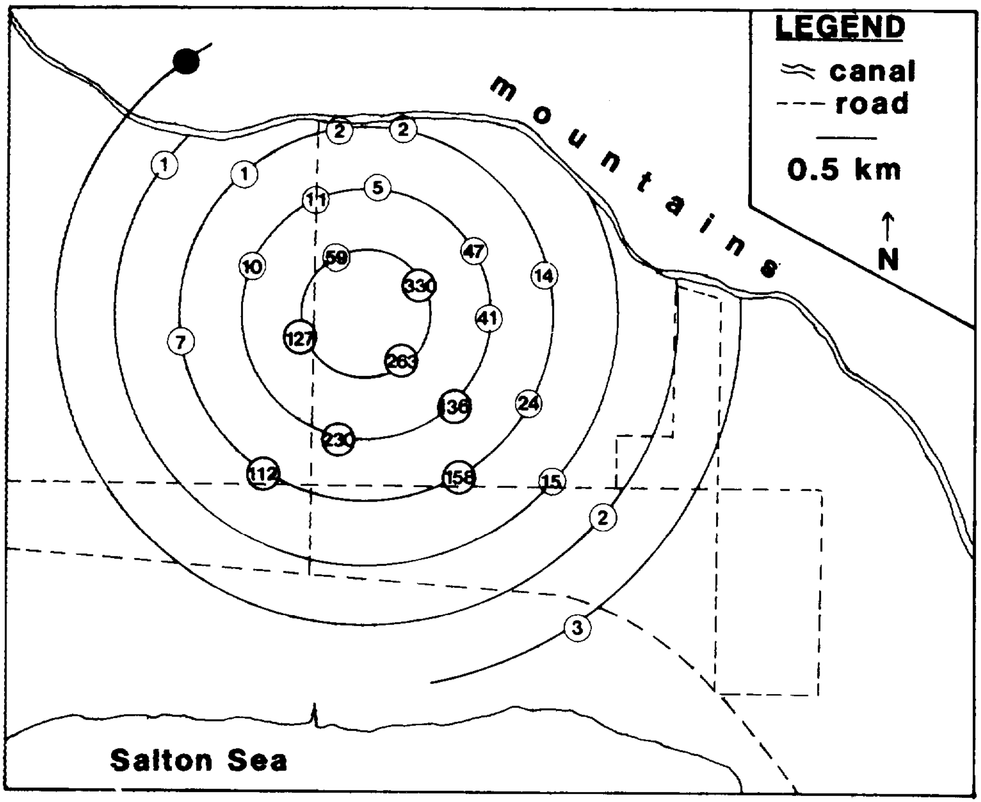
In order to compute MDT based on the results obtained with orange-marked females, some additional computations were necessary. Since all traps were within a 65° angle of the release point, the total area of a trap ring was multiplied by 0.18 (65/360), representing 18% of the total ring area. This value was used to determine the proportion of the total trapping area and the appropriate correction factor.

RESULTS

Host-seeking *C. mohave* females exhibited 2 peaks of activity, one occurring 1 hr after sunset (ss) and the other 1 hr before sunrise (sr) (Fig. 3). Rate of capture was greatest 1.1 km from the Salton Sea and least 5 km from the shoreline. At all 3 locations activity was low from 0030 to 0230 hr and host-seeking females were virtually absent during the day. Variations in wind speed during this period did not appear to affect host-seeking activity (Fig. 3).

The meteorological conditions recorded during our mark-release-recapture study are presented in Fig. 4. During the first 12 hr post-release (0100 to 1300 hr) conditions were "typically seasonal" with moderate temperatures, light and variable winds primarily out of the NNW. However, the approach and passing of a "cold" front caused marked changes from 1300

Fig. 1. Number of red-marked *Culicoides mohave* captured per trap location from (upper) 0 to 12 hr and 12 to 30 hr (lower) post-release at North Shore, CA, on September 29–30, 1981. Black disc indicates that no marked females were captured. The trap represented by a black star was removed at 12 hr; motor of the trap represented by a white star in a black disc failed during 12 to 30 hr.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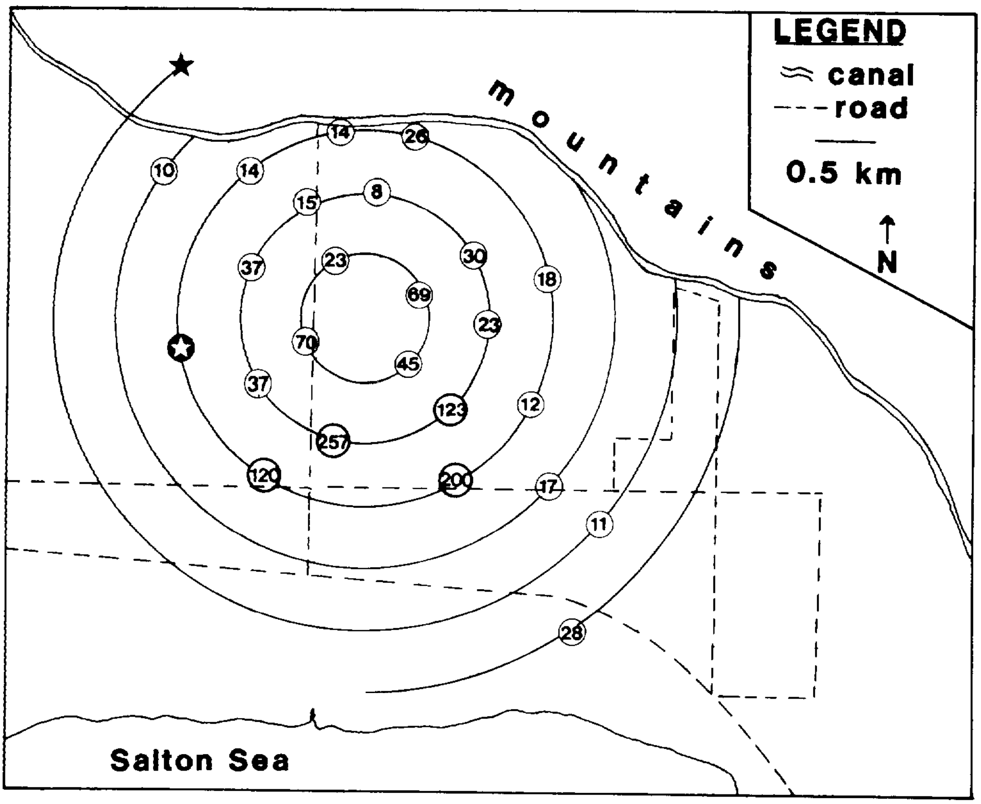
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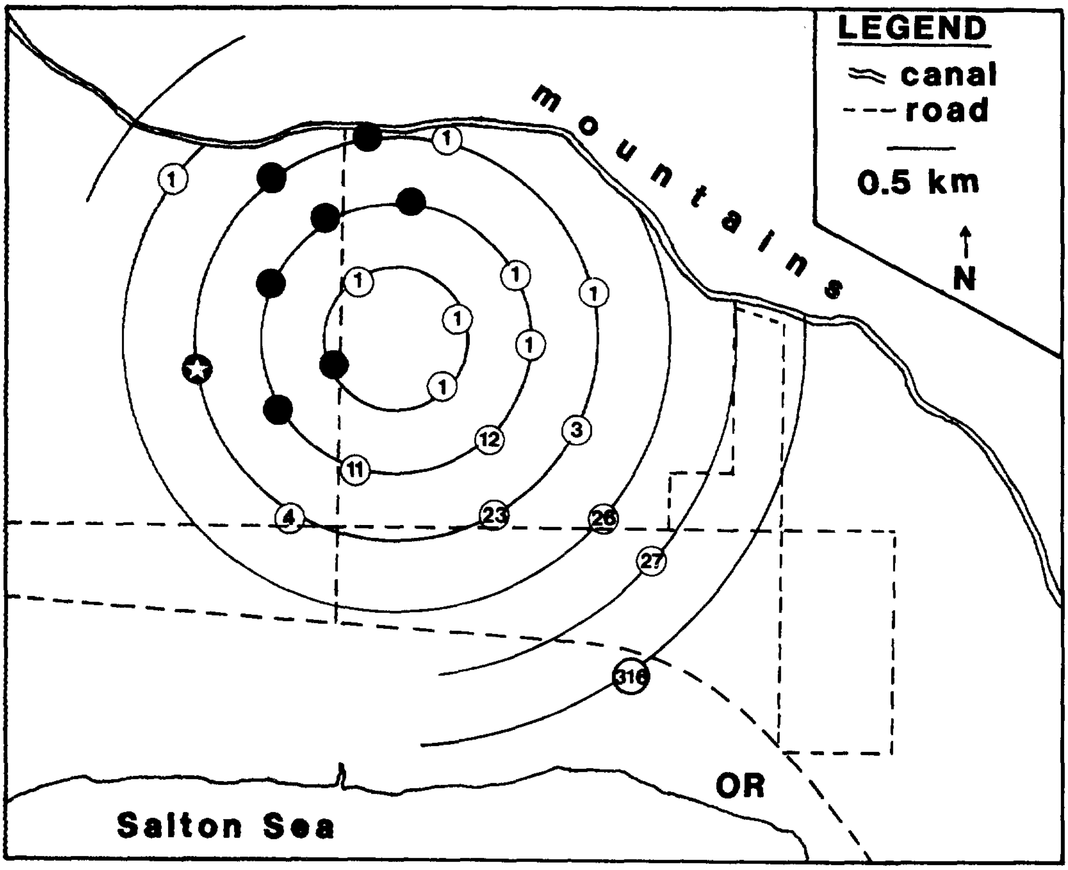

Fig. 2. Number of orange-marked *Culicoides mohave* captured per trap location from 12 to 30 hr post-release at North Shore, CA, from September 29–30, to October 1, 1981. OR = release point for orange-marked flies. Black discs represent traps that did not capture orange-marked females; motor of the trap represented by a white star in a black disc failed during 12 to 30 hr.

to 1700 hr (12 to 18 hr post-release). Winds increased in speed and changed from NNW to S. The passing of the front at 1600 hr was marked by high winds (note peak in Fig. 4) and a steady drop in temperature, although no rainfall occurred in the study area. By 1700 hr winds were diminished and variable, and by 2000 hr (when adults would begin their evening peak in activity), winds had again shifted to come from N. This trend prevailed throughout the remainder of the recapture study. Hence, during the periods in which host-seeking midges were active, winds prevailed from the N to NW.

Of the 20,646 red-marked *C. mohave* females released, we recaptured 2,794 (13.5%) (Table 1); only 2.6% (476/18,000) of orange-marked females were recovered. Within 12 hr post-release, all but 1 trap captured red-marked *C. mohave* females (Fig. 1a, upper). The exception was located on the far side of the freshwater Coachella Canal, 3.0 km from the point of release. Most recaptured females were taken in traps S and SE of the release point. From 12 to 30 hr post-release, the dispersed females were distributed more evenly, although 4 traps captured larger numbers S of the release point (Fig. 1b, lower).

The recapture rates by distance, and computed MDTs for red-marked females are presented in Table 1. From 0 to 12 hr post-release, 78.7% of the recaptured females were trapped within 1.0 km of the release point and 98.7% were within 1.5 km. The MDT, based on the corrected data, was 1.20 km in 12 hr. From 12 to 30 hr post-release, 77.5% of those recaptured were between 1.0 and 1.5 km from the point of release, while 5.6% had dispersed beyond 1.5 km. Thus, the population had dispersed further; MDT equaled 1.94 km.

Comparatively few orange-marked females were recovered; Fig. 2 illustrates the spatial

Table 1. Rates and distances of recapture during 2 collection periods following the release of 20,646 *Culicoides mohave* marked with red fluorescent dust near North Shore, CA, Sept.–Oct. 1981.

Trap ring radius (km)	Correction factor	Number recaptured		Corrected data	
		0–12 hr	12–30 hr	0–12 hr	12–30 hr
0.5	0.64	779	202	522	129
1.0	1.92	480	527	959	1012
1.5	3.19	320	399	1065	1272
2.0	4.47	16	27	74	120
2.5	5.74	2	11	12	63
3.0	7.04	3	28	22	197
Total		1600	1194	2654	2793
Mean distance traveled				1.20	1.94

distribution of those recaptured 12 to 30 hr post-release. Of these, 73% were collected in the trap nearest the release point (1.2 km) (Table 2). This trap, and the third from the release point (2.25 km) were the only traps to catch orange-marked females by 12 hr post-release (44 and 2, respectively; data not shown). At further distances the numbers of recaptured midges rapidly diminished. While 7% of those recaptured were beyond 3 km, only 3 females

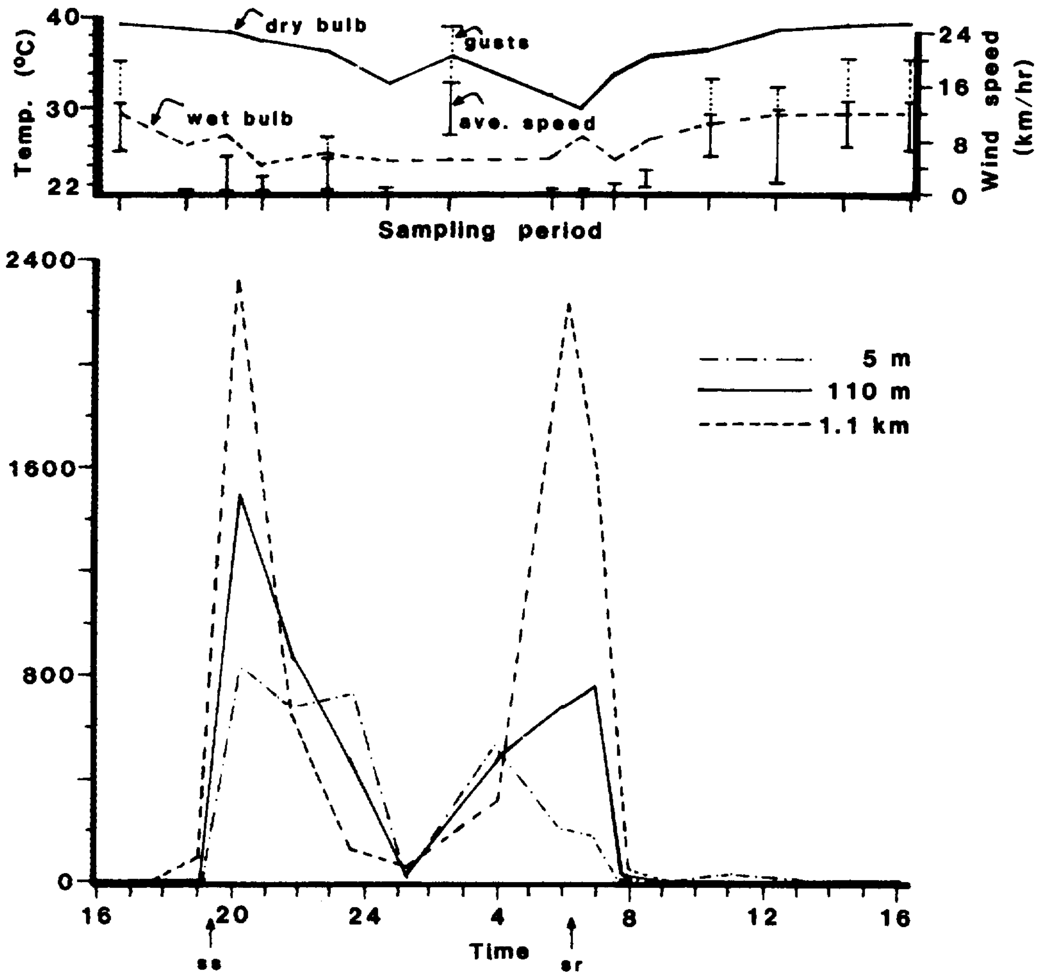

Fig. 3. Circadian activity of host-seeking *Culicoides mohave* as measured by the number captured per hour in 3 CO_2-baited surveillance traps at 3 distances from the Salton Sea at North Shore, CA, on August 24–25, 1981.

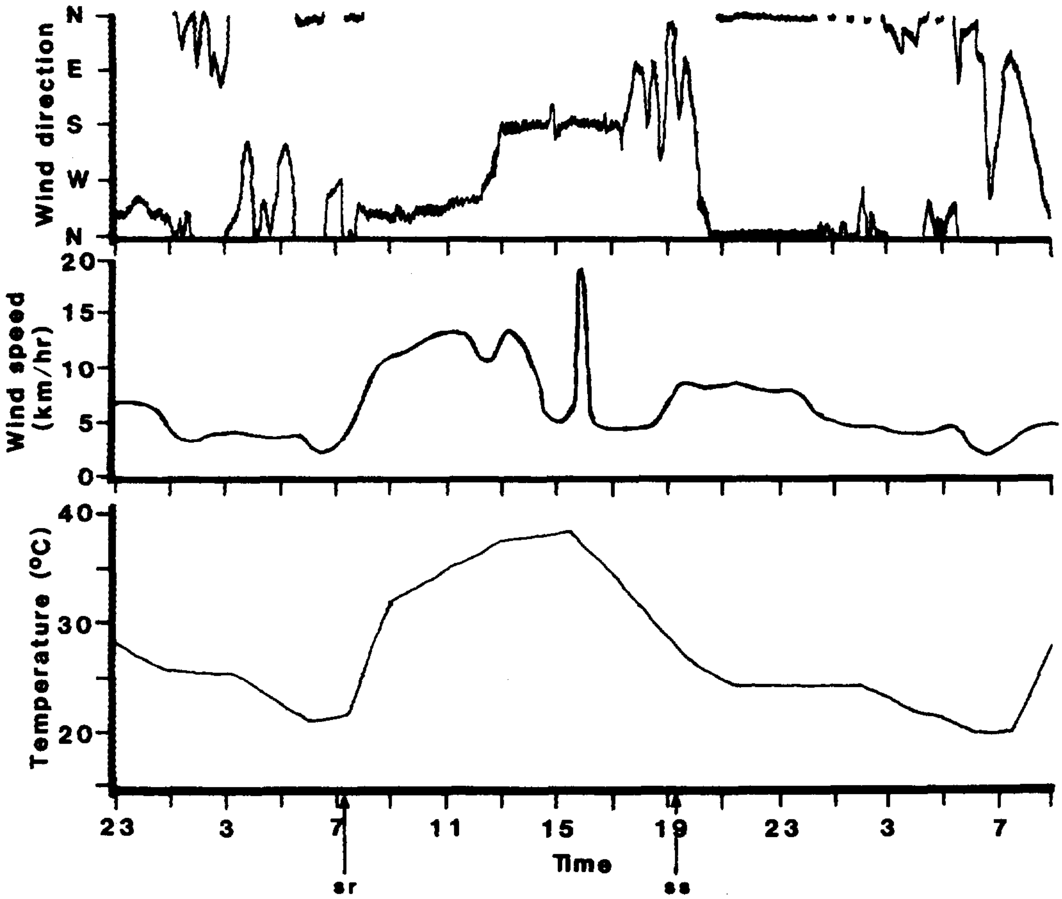

Fig. 4. Meteorological conditions during the mark-release-recapture of *Culicoides mohave* at North Shore, CA, during September 29–30, 1981. Measurements were recorded continuously at the point of release by a Meteorological Research Inc. weather station.

were collected at 4.5 km or beyond; the furthest at 6.0 km from the release point. Based on corrected data, the MDT in 30 hr by orange-marked females was 1.64 km.

Large numbers of unmarked *C. mohave* were captured. Trapping from 12 to 30 hr post-release fully encompassed 2 flight periods; hence, these data can be used to examine the spatial distribution of unmarked females (due to excessive trap-emplacement time (7 hr) not all traps sampled the peak period of activity during the first 12 hr post-release). Catch-density was unrelated to the order in which traps were changed ($r = -0.104$, $n = 23$, $P < 0.05$). The number captured per distance from the shoreline (i.e. larval habitat) is presented in Fig. 5. Excluding the trap closest to the larval habitat, catches tended to fall into 2 groups; mean values for traps between 1.0 and 2.5 km ($\bar{X} = 14{,}240$) differed significantly from the mean of traps > 2.5 km from the larval habitat ($\bar{X} = 2728.8$) ($t = 8.447$, $P << 0.01$, *t*-test for means with unequal variance and unequal sample sizes, Snedecor and Cochran (1967), data not presented). Data transformed to log catch versus distance indicated a strong correlation ($r = -0.92$, Fig. 5); however, a goodness of fit test, using the regression equation to generate expected values, was rejected ($\chi^2 = 16{,}895$, d.f. = 20), which traps within 2.5 km generally yielding more midges than predicted and traps at further distances collecting fewer than expected (see Fig. 5).

DISCUSSION

The movement of insect populations is variously referred to as dispersion or migration. There is general agreement, that migration refers to long distance, locomotory flight behavior, while the term dispersion is reserved for shorter movements involving activities such as

Table 2. Rates and distances of recapture from 12 to 30 hr following the release of 18,000 *Culicoides mohave* marked with orange fluorescent powder near North Shore, CA, Sept.–Oct. 1981.

Trap ring radius (km)	Correction factor	Number recaptured	Corrected data
1.20	0.92	316	290.7
1.75	1.04	27	28.1
2.25	1.28	26	33.3
2.75	1.59	26	41.4
3.25	1.92	12	23.0
3.75	2.24	18	40.5
4.00	1.24	2	2.4
4.50	2.71	1	2.7
5.00	3.04	0	0
5.25	1.64	1	1.6
5.50	1.72	0	0
6.00	3.66	1	3.7
Total		430	467.4
Mean distance traveled			1.64

feeding and reproduction (Johnson 1969, Dingle 1972). Species with restricted larval habitats, such as salt-marsh mosquitoes, commonly develop in large numbers and must disperse from the site of emergence to areas of greater host density (Provost 1952, 1957; Weaver and Fashing 1981). In an ecological sense, the Salton Sea in the midst of the Colorado Desert of southern California, is similar to the coastal salt marsh in that it offers a restricted and concentrated habitat. Larval ceratopogonids that have successfully exploited this environment can be found at enormous densities (Brenner et al. 1984, and unpublished data) and consequently, might be expected to disperse soon after emergence.

It seems likely that the small size of ceratopogonids (typically < 2 mm) and the harsh desert climate would preclude prolonged migratory flight, a characteristic of some salt marsh mosquitoes (Provost 1952). Our results on the circadian activity of *C. mohave*, although based on limited data, indicate that the density of host-seeking females is greatest at some unknown distance from the larval habitat, as opposed to being a strict hyperbolic relationship of decreasing density with increasing distance. A similar pattern was observed for *Leptoconops knowltoni* Clastrier and Wirth and *L. foulki* Clastrier and Wirth in this same area of the Salton Sea basin (Brenner et al. 1984). This distribution could be explained if newly emerged females are not prepared physiologically to seek a host until a short migratory flight has transpired. Our corrected data on the recapture of red-marked females provided some support for this speculation; a plot of corrected number versus distance clearly would not be hyperbolic, but would be more sigmoid in shape (see Table 1), indicating greatest densities between 1 and 2 km.

We have provided both empirical and experimental evidence suggesting that the main mass of a host-seeking *C. mohave* population readily disperses approximately 2 km or more. Within 30 hr, populations of marked host-seeking females dispersed a mean distance of 1.94 and 1.64 km with and against the wind, respectively. Our results from the release of the latter population, at a point peripheral to the

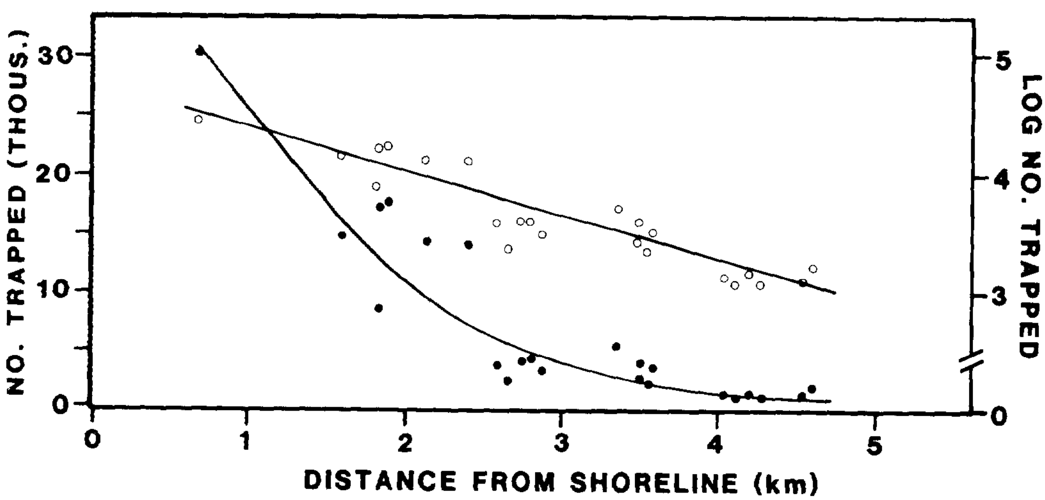

Fig. 5. Number of unmarked *Culicoides mohave* captured per trap location from 12 to 30 hr post-release of marked females at North Shore, CA, from September 30, to October 1, 1981. Plots represent number captured per trap (•) and log number captured per trap (o). Equation of linear regression line: log Y = 4.77 − 0.38X, r = −0.92.

concentric rings of traps, demonstrated that some (though not many) host-seeking females engaged in rather extensive dispersal (6.0 km in 30 hr) against the predominant movement of air. These data were further corroborated by our empirical observations on the spatial distribution of unmarked females; adults were captured throughout the Salton Sea basin, but the numbers diminished precipitously beyond 2.5 km.

Our data also revealed a change in the rate of dispersal over time. During the first 12 hr post-release, females, subjected to light winds from the NNW dispersed in all directions but primarily with the wind; the mean distance traveled was 1.2 km. During the next 2 periods of host-seeking activity the MDT increased, but at a lesser rate, to 1.94 km (a gain of only 0.74 km from 12 to 30 hr). Lillie et al. (1981) observed similar trends in the dispersal of *Culicoides variipennis*. It is possible that this change in the rate of dispersal is an artifact of omnidirectional flight which almost certainly would follow the initial "unidirectional" movement away from the point of release (Service 1976). Alternatively, this pattern may reflect actual changes in behavior, resulting from changes in the physiological state, as we have speculated.

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